Causal evidence for the role of the sensory visual cortex in visual short-term memory maintenance

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Abstract

The role of the sensory visual cortex during visual short-term memory (VSTM) remains controversial. This controversy is possibly due to methodological issues in previous attempts to investigate the effects of transcranial magnetic stimulation (TMS) on VSTM. This study aims to use TMS, while covering previous methodological deficits. Young adults will be recruited to participate in two experiments using a VSTM orientation change-detection under TMS. Monocular vision will be ensured using red-blue goggles combined with red-blue stimuli. Double-pulse TMS will be delivered at different times (Experiment 1: 0 ms, 200 ms, or 1000 ms; Experiment 2: 200 ms, 1000 ms) during a 2 s retention phase, on one side of the occipital hemisphere (right hemisphere for 50% of the participants). In experiment 2, a sham-TMS condition will be introduced. Behavioural effects in the ipsilateral occipital hemisphere to visual hemifield will indicate a causal involvement of the sensory visual cortex during a specific temporal point in VSTM.

Keywords: visual short-term memory, sensory visual cortex, working memory, sensory recruitment.

Visual short-term memory (VSTM) enables us to maintain in mind, for a short period of time, visual representations that are no longer present, in order to complete task-oriented goals. VSTM protects visual information against interference, making representations available for cognitive processing, and thus provides the essential link between perception and higher cognitive functions, underpinning our ability for complex thought and action (Luck & Vogel, 2013). For decades, cognitive scientists have studied the neural correlates of VSTM, establishing the role of specific brain areas such as the prefrontal and parietal areas in VSTM (Bettencourt & Xu, 2016; Christophel et al., 2017; Ester et al., 2015, Ester, Rademaker, et al., 2016; Funahashi, 2017; Lee et al., 2013; Mendoza-Halliday et al., 2014; Riley & Constantinidis, 2016; Smith & Jonides, 1999; Stokes, 2015; Xu, 2017, 2020, 2021). Although much research has attempted to understand the neural architecture of VSTM, it is still unclear if activity in the sensory visual cortex (area V1) is required for successfully maintaining visual information in short-term memory. Even though it is established that the sensory visual cortex is primarily engaged in encoding visual information (D'Esposito & Postle, 2015; de Graaf et al., 2014; Kamme, 2007; Serences, 2016, Xu, 2017), results are controversial when it comes to its involvement in VSTM maintenance (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Lorence Lorence & Sreenivasan, 2021; Serences, 2016; Sreenivasan et al., 2014; Tapia & Beck, 2014; Teng & Postle, 2021; van de Ven & Sack, 2013; Xu, 2017, 2020, 2021).

Traditionally, VSTM was investigated under the scope of sustained neural activity (Leavitt et al., 2017), suggesting that during VSTM tasks, neural activity potentials are maintained online in frontal and parietal cortical areas (e.g., Chafee & Goldman-Rakic, 1998; Funahashi et al., 1989). However, more recently this traditional view has been challenged (Lundqvist et al., 2018; Masse et al., 2020; Stokes, 2015) following methodological advances in computational methods of neuroimaging data. Specifically, using multivariate analyses, it has been shown that VSTM contents can be decoded in the sensory visual area, in the absence of sustained brain activity (Harrison & Tong, 2009; Serences et al., 2009). In addition, early visual brain areas were shown to respond to specific visual features during VSTM maintenance, such as orientation (Harrison & Tong, 2009; Issa

et al., 2008; Serences et al., 2009), contrast (Konstantinou et al., 2012), and direction of movement (Bisley & Pasternak, 2000). These findings led to the introduction of the sensory recruitment hypothesis, according to which the sensory visual cortex is an essential part of the brain network responsible for successfully maintaining information about elemental visual features in VSTM (Serences, 2016; Harrison & Tong, 2009; Pasternak & Greenlee, 2005; Postle, 2005; Serences et al., 2009; Supèr et al., 2001; for recent reviews see Lorence & Sreenivasan, 2021; Teng & Postle, 2021). In summary, this evidence indicated that early visual areas (such as area V1) have a dual function: they are involved in the precise sensory encoding of elemental visual features (e.g., contrast, orientation, spatial frequency, direction of motion, speed of motion), and the short-term maintenance of this information.

Indeed, sensory visual cortex neurons are ideal candidates for short-term maintenance because they exhibit highly selective tuning for specific visual features. Utilizing specialized regions of the visual cortex to support VSTM might be a highly efficient way to avoid recoding remembered information in other distal networks. Moreover, the high degree of the sensory visual cortex selectivity is not observed in higher-order areas, whereas such selectivity is critical for remembering subtle distinctions between stimuli. Even though evidence using multivariate analyses has supported stimulus-specific activation in frontal and parietal areas (Christophel et al., 2018; Ester, Sutterer, et al, 2016), this view has recently been contended (Postle & Yu, 2020). Yet, others have argued that storing information in sensory visual cortex leaves memory representations susceptible to overwriting as new stimuli are processed, and that networks in sensory areas are not sufficiently wired to support the type of recurrent activity thought to support VSTM (Xu, 2017, 2020, 2021). Given that higher-order brain areas lack the visual selectivity of early sensory areas, it is still unclear how people can maintain specific visual features, such as the precise orientation of a visual stimulus, with minimal decay over some seconds (Magnussen & Greenlee, 1999).

The controversial evidence regarding sensory recruitment (Awh & Jonides, 2001; Christophel et al., 2017; D'Esposito & Postle, 2015; Lorence & Sreenivasan, 2021; Serences, 2016; Sreenivasan et al., 2014; Tapia & Beck, 2014; Teng & Postle, 2021; Xu, 2017, 2020, 2021) has driven a debate in the current literature as to whether the sensory visual cortex is indeed involved in VSTM maintenance (Gayet et al., 2018; Scimeca et al., 2018) or whether its role is restricted to the perception of visual information (Xu, 2017, 2018, 2020, 2021). Specifically, Xu (2017, 2018, 2020, 2021) discussed that given the essential role of the sensory visual cortex during perception (see Awh & Jonides, 2001; D'Esposito & Postle, 2015; de Graaf et al., 2014; Kammer, 2007; Masse et al., 2020; Serences, 2016), information maintenance by the sensory visual cortex leaves representations susceptible to overwriting as it processes new incoming stimuli. To reaffirm sensory recruitment, counterarguments (e.g., Gayet et al., 2018; Scimeca et al., 2018), proposed that the sensory visual cortex protects representations by utilizing processes, such as between layer top-down signals in area V1 (van Kerkoerle et al., 2017; Zhao et al., 2021). These processes were described as being similar to those employed by the prefrontal cortex during attention modulation (see Scimeca et al., 2018), when differentiating between mnemonic and perceptual information (e.g., Knight et al., 1999). Additionally, it has been proposed that the interaction between memory representations and perceptual input might be beneficial instead of detrimental to VSTM. For example, VSTM representations can improve perceptual continuity and goal-related behavior by biasing perceptual input (Gayet et al., 2013; Kiyonaga et al., 2017). Further, Xu (2017) pointed out that the sensory visual cortex is not sufficient to support sustained VSTM activity and sustained activity recorded in the sensory visual cortex most likely relates to feedback from higher order brain areas. However, alternative explanations proposed that sustained activity in the prefrontal cortex, might echo a biasing signal to protect or direct attention towards goal related VSTM representations, rather than reflect VSTM representations per se (Curtis & D'Esposito, 2003; Sreenivasan & D'Esposito, 2019; Masse et al., 2020; Miller & Cohen, 2001; Sreenivasan et al., 2014).

To explore sensory recruitment, researchers have implemented many methodological approaches, such as functional magnetic resonance imaging (fMRI) and psychophysical experiments, but have yielded mixed results (e.g., Bettencourt & Xu, 2016; Harrison & Bays, 2018; Rademaker et al., 2019; Yörük et al., 2020). Several reasons have been proposed to explain these mixed results, such as activity silent mechanisms, feed-forward processes, lack of causal evidence, methodological differences and in some cases methodological oversights (D'Esposito et al., 1999; D'Esposito & Postle, 2015; Lorence & Sreenivasan, 2021; Masse et al., 2020; Serences, 2016; Teng & Postle, 2021; Xu, 2017, 2020, 2021). An ideal hypothetical scenario for investigating whether sensory visual cortex is required for VSTM maintenance would involve its complete inactivation during the retention interval of a VSTM task and reactivation at the onset of the memory probe display (Gayet et al., 2018). Such an experimental design could yield causal evidence as to whether the sensory visual cortex is a necessary component of the brain network responsible for the short-term maintenance of elemental visual features. Although such an experiment is impossible to be carried out, brain stimulation using transcranial magnetic stimulation (TMS) during the retention interval of a VSTM task can approximate this scenario. TMS uses a coil to transfer electromagnetic stimulation at localized brain areas. TMS targeted at the sensory visual cortex has been shown to directly interfere with cortical activity, making the exploration of causal evidence plausible (de Graaf et al., 2014; Pitcher et al., 2020; Tapia & Beck, 2014).

Previous studies have attempted to investigate the role of the sensory visual cortex in VSTM using TMS, combined with delayed change detection or match-to-sample tasks (Cattanea et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). In these tasks, a memory array (i.e., set of stimuli that participants are asked to remember) is presented to participants, followed by a maintenance delay period. Subsequently, participants are requested to compare (or match) a probe with the earlier memory array. The sensory visual cortex is stimulated at different points during the maintenance delay period, in order to make causal inferences based on the temporal point of the TMS

interference. In most experiments, stimulation was induced on the sensory visual cortex of one hemisphere, while stimuli were presented either in the ipsilateral or contralateral (to the stimulation site) visual hemifield in a counterbalanced manner (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017). To draw evidence and reach a conclusion, comparisons between the ipsilateral versus the contralateral conditions (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven & Sack, 2012; van Lamsweerde & Johnson, 2017), and between real versus sham TMS (Cattaneo et al., 2009; Jia et al., 2021; Rademaker et al., 2017; Silvanto & Cattaneo, 2010) were considered.

As with different methodological approaches, results from previous TMS studies were mixed with regards to the sensory recruitment hypothesis. Specifically, some of the studies supported the sensory recruitment hypothesis (Cattaneo et al., 2009; Jia et al., 2021; Silvanto & Cattaneo, 2010), some rejected it (Rademaker et al., 2017; van Lamsweerde & Johnson, 2017), while others were unclear (van de Ven et al., 2012). After a careful examination of the methods used in previous TMS studies, we suggest that the inconclusive findings are due to several important methodological issues that may have underestimated the contribution of the sensory visual cortex in VSTM. The most vital issue in the majority of these TMS studies is that previous researchers considered that, when information was presented on one side of the visual hemifield (either right or left side near the centre of the monitor), the information was processed by the contralateral sensory visual cortex. Therefore, stimuli were always presented binocularly to the participants either in the left or right visual field, and a contralateral sensory visual cortex TMS was applied and compared to an ipsilateral control condition (see Figure 1A). However, considering the neuroanatomy of the visual pathway system, the binocular presentation of stimuli either left or right close to the midline of the visual field -as was the case in the majority of the previous studies- does not accurately correspond to the contralateral sensory visual cortex, and could in fact be processed by the ipsilateral one if presented withing 15° of visual angle from midline (Joukal, 2017; Wichmann & Müller-Forell, 2004). It is also possible that information enters the sensory visual cortex in both brain's hemispheres (Tong et al.,

2006; Zhao et al., 2021) since the visual fields of both eyes overlaps in certain areas (within 15° of visual angle, see Figure 1B; Wichmann & Müller-Forell, 2004). Consequently, some TMS effects can be falsely interpreted or remain undetectable (e.g., if information processing happens in both hemispheres despite the contralateral and ipsilateral conditions; de Graaf & Sack, 2011; see also Pitcher et al., 2020). For example, as pointed out in a recent review of the sensory visual cortex TMS VSTM literature (Phylactou et al., 2021), a study considering the contralateral TMS condition as the experimental condition and the ipsilateral side as the control condition will interpret a performance drop (e.g., contralateral performance < ipsilateral performance) as an inhibitory TMS effect. Though, considering the evidence supporting the role of the ipsilateral sensory visual cortex in visual processing (Zhao et al., 2021) and the neuroanatomy of the visual pathway (Wichmann & Müller-Forell, 2004), it is possible that the ipsilateral sensory visual cortex is in reality the experimental condition. As such, the conclusion of the same study, might turn out to be the opposite (e.g., facilitation effects since ipsilateral accuracy > contralateral accuracy), if the experimental and control conditions are inversely defined.

Another important shortcoming relates to the complexity of the stimuli used in the memory array. In a given memory array, there is a minimal representational requirement for VSTM, based on the core features (e.g., color, orientation, shape) of stimuli (Alvarez & Cavanagh, 2004). A greater combination of stimuli features increases complexity and VSTM capacity requirements. Previous TMS studies used various stimuli in their memory tasks, some of which were complex stimuli such as abstract shapes (van de Ven et al., 2012). However, the evidence leading to the sensory recruitment hypothesis emphasized the selective engagement of the sensory visual cortex in elemental visual features such as orientation, contrast, and direction of movement (Harrison & Tong, 2009; Issa et al., 2008; Konstantinou et al., 2012; Serences et al., 2009). For example, Jia and colleagues (2021), indeed found a strong TMS effect in a VSTM task requiring participants to remember the elemental visual feature of orientation of one grating, but in a study requiring participants to remember either one (low load) or three (high load) abstract shapes (that are thought to be complex stimuli consisting

of a combination of elemental visual features; van de Ven et al., 2012), TMS did not affect

performance in the low load condition of remembering a complex shape (TMS effects were only

evident during the three-item high load condition). Such findings are suggesting that when stimuli

complexity increases, higher order brain areas might be more actively recruited for VSTM, such as

the intraparietal sulcus (Xu & Chun, 2006; Xu, 2007) and the posterior parietal cortex (Song & Jiang,

2006). Thus, the neural processes required for successfully maintaining complex visual stimuli in

VSTM might be more dependent on higher order brain areas than simple stimuli consisting of

elemental visual features, given the high selectivity of sensory visual cortex in processing of

elemental features (Teng & Postle, 2021). This might explain some of the null effects of sensory

visual cortex TMS during the memory delay, since complex representations are likely protected

through a more distributed VSTM network (Lorenc & Sreenivasan, 2021; see also Gayet et al., 2018;

Scimeca et al., 2018). Hence, it is possible that some of the previous studies failed to find evidence

for the sensory visual cortex involvement in VSTM due to using such more complex stimuli.

Therefore, in order to provide causal evidence for the role of the sensory visual cortex

during VSTM more reliably, the methodological limitations of previous TMS studies need to be

addressed. In particular, the two visual hemifields must be reliably separated so that the visual input

is processed by only one occipital hemisphere. One way to reliably separate the sensory visual cortex

hemisphere that processes the information entering the visual field is to present the stimuli

monocularly. To achieve monocular stimulus presentation, similar methodological principles as

those used in binocular rivalry can be implemented (Carmel et al., 2010). In binocular rivalry,

different images overlapping in the visual field are presented separately to each eye. Therefore, by

presenting an image corresponding only to one eye (thus avoiding rivalry), stimuli will enter the

sensory visual cortex monocularly (Polonsky et al., 2010). Also, given the V1 neuronal response to

specific visual features, the memory array should consist of an elemental visual feature known to

selectively correspond to the sensory visual cortex, such as orientation (Harrison & Tong, 2009; Issa

et al., 2008; Jia et al., 2021; Serences et al., 2009; Swisher et al., 2010).

Previous TMS studies, stimulated the sensory visual cortex at various timepoints during VSTM maintenance, with variable results (e.g., Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017; for reviews see Phylactou et al, 2021; Xu, 2017). For example, Rademaker et al. (2017) interfered with sensory visual cortex TMS at 0 ms and 900 ms into the delay period, van Lamsweerde et al. (2017), at 0 ms, 100 ms, and 200 ms, and van de Ven et al. (2012) at 100 ms, 200 ms, and 400 ms. Some studies indicated that TMS effects were stronger for earlier stimulation (up to 200 ms; Rademaker et al., 2017; van Lamsweerde et al., 2017), compared to later stimulation at 400 ms (van de Ven et al. 2012), and 900 ms (Rademaker et al., 2017), however other studies indicated that TMS after 200 ms was stronger (van de Ven et al., 2012). Based on a recent meta-analysis examining the effects of TMS on VSTM performance during the maintenance period, most studies differentiated between earlier (up to 200 ms into the maintenance period) and later (after 200 ms; usually at the middle of the maintenance period) stimulation (Phylactou et al., 2021). In the current work, we similarly differentiated between early and late TMS, by considering the outcomes of previous studies (Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde et al., 2017), in order to replicate and explore any similar findings concerning a different TMS effect size for earlier compared to later stimulation. Thus, we will examine the effects of TMS on behavioral performance separately for stimulation induced at 200 ms and 1000 ms (halfway) into the delay period.

In short, the objective of the current study is to provide causal evidence for the role of the sensory visual cortex during VSTM maintenance using TMS, while ensuring monocular vision. In the proposed experiments, stimuli will be presented in the center of the visual field to be viewed monocularly. Therefore, based on the neuroanatomy of the visual pathway (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-Forell, 2004), it is expected that visual information will initially be processed solely by the ipsilateral (to the eye receiving the information) sensory visual cortex. As a result, and contrary to past experiments, the contralateral sensory visual cortex will be the control condition. To explore our main question of whether the sensory visual cortex is involved in VSTM maintenance, our hypotheses focus on testing differences in detection sensitivity (Stanislaw &

Todorov, 1999) in a VSTM task, between the ipsilateral and contralateral conditions when stimuli are presented monocularly and TMS is applied (1) during perceptual processing (outcome neutral condition; 0 ms after stimulus onset), (2) during early information maintenance (200 ms after stimulus onset), or (3) during late information maintenance (1000 ms after stimulus onset). Moreover, in a second experiment, we will test whether VSTM performance differs between a TMS and a sham TMS condition (1) during early information maintenance (200 ms after stimulus onset) and (2) during memory late information maintenance (1000 ms after stimulus onset). Table 1 presents a detailed description of the research hypotheses for each experimental condition.

Methods

Ethics information

The study has been approved by the Cyprus National Bioethics Committee (ЕЕВК/ЕП/2016/37).

Design

Apparatus and stimuli

A Magstim Super Rapid[2] (MagStim, Whitland, Wales, UK SA34 OHR) stimulator will be used for inducing TMS. A Magstim D70 Alpha Flat Coil (Uncoated) will deliver a double-pulse TMS at the different experimental conditions, while a sham coil will be used to control for noise and other TMS artefacts (in Experiment 2). The sham coil will look identical to the D70 Alpha Flat Coil, but it is equipped with thicker shield, restricting it from inducing magnetic fields, which interfere with brain activity. The double-pulse TMS will be induced with a frequency of 10 Hz, meaning that stimulation will be delivered by two pulses separated by a duration of 100 ms. A 10 Hz double-pulse TMS was chosen to ensure the reliability of the outcome neutral condition. Specifically, the first pulse will be induced at the beginning of stimulus presentation and the second pulse at stimulus offset (see below). Given the possibility that a long encoding time (~100 ms) can lead to successful consolidation despite masking interference (Ye et al., 2017, 2021; Zhang & Luck, 2008), the double-

pulse TMS will ensure that interference with regular brain activity is introduced throughout the

consolidation process (Ye et al., 2017, 2021). For comparison and consistency reasons, the double-

pulse TMS will be used in all experimental conditions. The stimuli and all experimental procedures

will be designed and controlled using Python and PsychoPy (Peirce et al., 2019), which will be run on

an HP PRODESK desktop computer. To control the TMS, the MagPy TMS package will be used

(McNair, 2017). Stimuli will be presented on a 21.5" Philips 226V[la] monitor with a 60 Hz refresh rate.

A chinrest will be placed to ensure that participants maintain a viewing distance of 57 cm from the

monitor. Stimuli will consist of either a red (RGB: 255, 0, 0) or a blue (RGB: 0, 0, 255) Gabor patch

which will be oriented either horizontally or with a clockwise or counter-clockwise tilt from the

horizontal axis, presented on a black (RGB: 0, 0, 0) background (Figure 2). The Gabor patch will

consist of a gaussian envelope with a standard deviation of 0.39° (in degrees of visual angle), 0.001°

frequency, and have a 1° diameter. Stimuli will be presented at fixation. To ensure that stimulus will

be viewed monocularly, stimuli will be viewed through red/blue anaglyph goggles, consistent with

previous research (Haynes et al., 2005), where red stimuli will only be viewed by the left eye and

blue stimuli only by the right eye (Carmel et al., 2010).

Experimental design

Two experiments using the same delayed change-detection task will be carried out.

Participants will be asked to compare the orientation of a probe to the orientation of a remembered

grating (memory array) after a 2 second delay period (Figure 2). In half the trials, the probe will have

the same orientation as the memory array. In the other half, the probe will be oriented clockwise

(25% of the trials) or counter-clockwise (25% of the trials) to the remembered grating (Figure 2).

Experiment 1 is designed to allow for within-subject comparisons between the ipsilateral

and contralateral stimulation conditions at three different TMS timing conditions. Timing conditions

refer to the temporal distance of the stimulation after the memory grating's onset. The 0 ms timing

condition, will work as an outcome neutral test measurement to confirm that our method is reliable

to detect TMS effects. Specifically, the first TMS pulse is induced at the onset of the stimulus and the second TMS pulse when the stimulus presentation finishes (at 100 ms). Thus, given the established role of the sensory visual cortex during visual perception (D'Esposito & Postle, 2015; de Graaf et al., 2014; Kamme, 2007; Serences, 2016, Xu, 2017), a significant difference in VSTM performance is expected in the ipsilateral compared to the contralateral condition (either facilitation or inhibition; for details see Table 1). The 200 ms condition (first TMS pulse at 200 ms after stimulus onset and second TMS pulse 300 ms after stimulus onset) will shed light on the role of the sensory visual cortex during the early maintenance phase of VSTM, while the 1000 ms condition (first TMS pulse at 1000 ms after stimulus onset and second TMS pulse 1100 ms after stimulus onset) will allow the exploration of its role during the later maintenance period. These conditions lead to a two (ipsilateral/contralateral) by three (0ms/200ms/1000ms) design. A total of 360 trials (120 trials per timing condition; 60 with ipsilateral TMS and 60 with contrallateral TMS in each timing condition) will be gathered, which will be divided into six blocks of 60 trials and presented in a counterbalanced manner across participants.

Experiment 2 aims to replicate the effects that will be obtained in Experiment 1, while controlling for other factors that may cause or hinder our experimental effects, by adding a sham-TMS control condition. In addition to controlling for TMS noise and other artefacts, a sham TMS control is important for three reasons. First, TMS interference may affect both hemispheres due to the visual input being processed by both hemispheres and thus any actual effects remain undetected (de Graaf & Sack, 2011; Pitcher et al., 2020). Since Experiment 1 compares an ipsilateral with a contralateral condition, where stimulation is always present, it is plausible that TMS noise interferes in such a way, that an effect in behaviour is always present. Thus, if the additional noise by TMS affects the baseline condition, then comparisons between the ipsilateral and contralateral stimulation condition might not indicate any significant difference. By introducing a sham TMS condition, Experiment 2 will control for this possibility, allowing comparisons between real and sham stimulation. Second, it is likely that the sensory visual cortex processes information in both

hemispheres (e.g., due to feedforward and feedback mechanisms; King & Wyart, 2021; Zhao et al.,

2021) so that stimulating only one of the two hemispheres is not enough to affect behavioural

measures. Lastly, contrary to previous research, we suggest that visual information will be initially

processed by the ipsilateral sensory visual cortex when the stimulus is presented within

approximately 15° of visual angle from midline (Joukal, 2017; Tong et al., 2006; Wichmann & Müller-

Forell, 2004). However, without a sham control condition, it would be impossible to correctly

interpret the direction of any possible effect. Specifically, in previous experiments, TMS was shown

to either facilitate (Cattaneo et al., 2009) or hinder (Jia et al., 2021; van de Ven et al., 2012)

performance. It should be pointed out, that the interpretations of such effects are unavoidably

biased by the hypotheses. For example, if an effect is expected in the contralateral site, an increased

performance might be interpreted as a facilitation effect but might, in reality, be due to hindering

effects in the ipsilateral condition. Thus, given the neural basis of the visual pathway (Joukal, 2017;

Tong et al., 2006; Wichmann & Müller-Forell, 2004), along with the possible feedforward and

feedback mechanisms of the sensory visual cortex (e.g., Miller et al., 1996; Van Kerkoerle et al.,

2017; see also King & Wyart, 2019), this is an important factor that must be controlled for.

Therefore, Experiment 2, will allow comparisons between actual and sham stimulation on behaviour.

Since sham TMS is introduced in Experiment 2, which will work as a baseline measurement, the 0 ms

condition that was used as an outcome neutral condition in Experiment 1 will be dropped.

Therefore, in Experiment 2, only two timing conditions will be used, at 200 ms (first TMS pulse at

200 ms after stimulus onset and second TMS pulse 300 ms after stimulus onset) and 1000 ms (first

TMS pulse at 1000 ms after stimulus onset and second TMS pulse 1100 ms after stimulus onset),

corresponding to an early maintenance phase and a late maintenance phase of VSTM respectively.

As in Experiment 1, the timing conditions refer to the temporal distance between stimulation and

memory array onset. This leads to a within-subject design, comparing differences between the

ipsilateral and contralateral conditions, at two different TMS timing conditions, and two different

stimulation conditions. These conditions create a two (ipsilateral/contralateral) by two (200

ms/1000 ms) by two (TMS/sham TMS) design. In total, 512 trials (256 TMS conditions; 128 per

timing condition out of which 64 ipsilatteraly and 64 contrallateraly and 256 sham TMS conditions;

128 per timing condition 64 ipsilatteraly and 64 contrallateraly) will be collected, which will be

divided into eight blocks of 64 trials and presented across participants in a counterbalanced fashion.

Procedure

      Sensory visual cortex stimulation. Before the main experiment, we will localize the right or

left sensory visual cortex of each participant (Cattaneo et al., 2009; Silvanto & Cattaneo, 2010; van

de Ven et al, 2012) using the functional method of eliciting phosphenes (Walsh & Pascual-Leone,

2003) and the localization will be counterbalanced across participants. Specifically, a tight cap will be

placed on each participant's head and the inion will be marked. Participants will be blindfolded but

instructed to keep their eyes open using a hollow blindfold. The coil will be placed two centimetres

above the inion and one centimetre laterally (either left or right based on the participant's group).

Starting at a 60% TMS output power, a double-pulse TMS will be delivered and participants will

orally report whether they have seen phosphenes or not (by saying outloud "yes" or "no"). If no

phosphenes are reported after three consecutive stimulations, the procedure will be repeated by

moving the coil in a one-by-one centimetre grid around the initial stimulation point by

approximately 0.2 centimetres, inducing three single-pulse TMS at each position. If a participant still

fails to report phosphenes, the same procedure will be repeated with a 5% increase on the

stimulator output until phosphenes are reported, or until an 80% power on the stimulator has been

reached. If participants fail to report phosphenes, the localization procedure will be repeated on the

opposite cortex and if they still fail to perceive phosphenes, a fixed output set at 65% of the

stimulator's maximum output will be used, as has been done previously (Cattaneo et al., 2009;

Koivisto et al., 2017; Saad et al., 2015). When the participants successfully report phosphenes, a

mark will be placed on the cap and a mechanical arm will stabilize the TMS coil and together with

the chinrest, this will hold the participant's head stable on that point. The TMS coil will be stabilized

at the position where participants report phosphenes as close to the center of the visual field as

possible, thus overlapping with stimulus presentation. Three additional single pulses will be induced

to confirm that participants experience phosphenes, and thus the coil is placed correctly. Halfway

through the experiments (after 3 blocks in Experiment 1, and after 4 blocks in Experiment 2),

participants will be blindfolded again, and three single pulses will be induced on the mark, to confirm

the induction of phosphenes and consequently stable coil placement. During this process, and if

necessary, phosphene localization will be repeated, in order to adjust for possible drifts.

After localizing the sensory visual cortex, we will estimate each participant's individual

threshold by determining the required stimulation power output for perceiving phosphenes using an

adjusted staircase method (Cornsweet, 1962). With the use of custom code, double-pulse TMS

stimulation will be induced on the localised sensory visual cortex at different stimulation output

powers, and participants will respond whether they have seen phosphenes or not via button press.

Given their responses, the power will decrease (if they report phosphenes twice on a specific TMS

power output consecutively) or increase (every time they fail to report phosphenes). Calculations

based on the mean of the intervals where the power output changes direction (i.e., from higher

power to lower or vice versa) will produce an approximation of the stimulation power required to

elicit phosphenes 50% of the time the sensory visual cortex is stimulated. Because this procedure

will be done with a blindfold over participants eyes, stimulation power in the main experiments will

be set at 110% of the estimated threshold stimulation power to adjust for visual exposure that can

affect the phosphene threshold (Boroojerdi et al., 2000).

To account for individual differences and avoid ceiling or floor effects in task performance,

additional procedures will be conducted before the main experiments. Specifically, the task will be

adjusted to each participant's perceptual ability to discriminate between orientation changes. A

custom staircase procedure will be implemented, where participants will have to report whether a

grating has a clockwise or counterclockwise tilt from the horizontal axis. According to each

participant's responses, the degrees of this tilt will either decrease (when three consecutive correct

responses are given) or increase (when a response is incorrect). An approximation of accurately discriminating the orientation difference 75% of the time will be obtained by calculating the mean of the intervals where degree differences change direction (i.e., from an increase in degrees to a decrease and vice versa). The gratings used in this staircase will be identical to the experimental stimuli and so this procedure will be done twice, separately for the blue and red stimuli. For the main experiment, the orientation thresholds both for the red and blue stimuli will be increased by 20%, to account for the increased cognitive demands of the main task. Furthermore, before the two main experiments, participants will carry out a practice block of 24 trials without TMS stimulation to familiarize themselves with the experimental procedure. If accuracy in the practice block is less than 75%, the practice block will be repeated until the participant reaches at least 75% accuracy. Participants will be replaced if after four practice blocks their accuracy remains below 75%.

Experiment 1. Each trial will begin with a screen indicating the trial number for each block. To proceed to the next trial, participants will need to press the 'spacebar' key on the keyboard. Next, a 500 ms white fixation dot will appear on the centre of a black background, followed by the memory grating for 100 ms. The stimulus grating will either have a horizontal orientation (50% of trials), a clockwise (25% of trials) or counter-clockwise (25% of trials) tilt. The tilt angle will be fixed across all trials for each participant at the level determined using the staircase procedure described above. From stimulus onset, a 2000 ms delay period indicated by a centred fixation dot will follow. Double-pulse TMS will be pseudorandomly delivered at one of three different timing conditions after the memory onset; either 0 ms, 200 ms, or 1000 ms. At the end of the retention period, a probe stimulus will appear. In half trials, the probe will be the same as the memory array stimulus. In the remaining 50% trials, the probe will be different as follows: if the memory array was horizontal, the probe will be tilted clockwise (25% of the different-condition trials) or counter-clockwise (25% of the different-condition trials). If the memory array stimulus was tilted, then the probe will be horizontal (50% of the different-condition trials). Participants will have up to 3000 ms starting at probe onset to respond by placing their index and middle fingers on the arrow keys on the keyboard, indicating

whether the orientation of the probe is the same (index finger; 'left arrow key') or different (middle finger; 'down arrow key') compared to the memory array grating. Feedback will be provided only in the cases of no response or an incorrect response, by presenting the word 'Wrong!' in red letters in the center of the screen for 1000 ms.

Experiment 2. The second experiment will use the same delayed change-detection VSTM task as in Experiment 1. The difference in Experiment 2 is the introduction of a sham coil that will deliver sham stimulation. TMS and sham TMS conditions will be blocked in a counterbalanced order. In addition, given the sham TMS condition, the 0 ms condition, which works as an outcome neutral test, will be dropped. At the end of the experiment, participants will self-report whether they noticed any differences between sham TMS and TMS.

Sampling plan

Healthy undergraduate and graduate students from the Cyprus University of Technology will be recruited to participate voluntarily. Only individuals with normal or corrected to normal vision will be included in the study. Prior to participation, participants will be screened for colour deficiencies using the 10-item screening edition Ishihara Colour Deficiency Test, and any individual who shows signs of colour blindness will be excluded from the study.

For Experiment 1, sample updating with a stopping rule has been set to $BF_{10} > 6$ or $< 1/6$ for all three paired t-tests that will be performed. However, due to counterbalancing, a minimum of 20 participants will be gathered (to ensure counterbalancing) or a maximum of 40 participants, given time and resource constraints. Specifically, after data collection for the first 20 participants is completed, we will perform our analyses to check if the stopping rule has been fulfilled. If any of the three BFs did not reach the stopping rule of > 6 or < 1/6, we will recruit four more participants and repeat the analyses. This process will be repeated until all three BFs fulfil the stopping rule, or until the maximum of 40 participants is reached. A similar sample updating process with a stopping rule ($BF_{10} > 6$ or $< 1/6$) is set for all four paired t-test of Experiment 2. Similar to Experiment 1, a minimum

of 20 participants will be gathered (to ensure counterbalancing) or a maximum of 40 participants

(due to constraints) for Experiment 2. Therefore, the total number of participants for both

experiments will range between 40 to 80 participants.

Analysis plan

Analyses will be conducted using Jamovi (The Jamovi Project, 2021), an openly available R-

based statistical software.

Experiment 1. The TMS site (ipsilateral vs. contralateral) will be the independent variable in

Experiment 1. Since monocular vision will be ensured, the ipsilateral condition refers to the situation

where the TMS localised site (for example, right sensory visual cortex) is on the same side as the eye

processing the stimulus (for example, right eye, and consequently the blue stimulus). The

contralateral condition corresponds to when the TMS localised site (for example, right sensory visual

cortex) does not match the side of the eye processing the stimuli (for example, left eye, and

consequently red stimulus).

The main dependent variable that will be considered is *d'*. The *d'* variable is a signal

detection theory indicator of detection sensitivity calculated by subtracting the standardised false

alarm rate of responses from the standardised hit rate:

$$d' \, = \, z(H) - z(FA)$$

where *H* is the Hit rate (i.e., correct responses of the probe being the same as the memory array

grating) and *FA* is the False Alarm rate (i.e., incorrect responses of the probe being the same as the

memory array grating). These rates correspond to probabilities on the normal distribution, therefore

z(H) and *z(FA)* are the *z-scores* that correspond to the normal distribution's tail p-values represented

by *H* and *FA*.

In Experiment 1, we will perform three Bayesian paired t-tests in order to calculate a Bayes

Factor; one t-test on TMS stimulation site (ipsilateral *d'* vs. contralateral *d'*) for each of the three

TMS timing conditions (0 ms, 200 ms, 1000 ms). Each t-test will examine if the difference between the ipsilateral *d'* and contralateral *d'* differs from zero. The Bayes Factor will indicate the likelihood ratio of each alternative hypothesis over the null hypothesis (BF_{10}), thus providing evidence for the likelihood of both hypotheses (see Table 1). The 0 ms timing condition works as an outcome neutral test or positive control condition, in order to test our methods. Given that the effect of TMS might affect both hemispheres and/or that the sensory visual cortex processing information in both hemispheres through feedforward and feedback processes, it is possible that TMS effects between hemispheres remain undetected with our proposed methods. This possibility will be tested in Experiment 2, with the introduction of sham TMS condition and statistical tests between real versus sham TMS across hemispheres. The 200 ms and 1000 ms timing conditions would test whether the sensory visual cortex is involved during early and late maintenance of visual information, respectively.

Each prior for the paired t-tests is described by a Cauchy distribution centered around zero (see Rouder et al., 2009). Each prior was based on the results of a recent meta-analysis on the topic (Phylactou et al., 2021), which reported the standardised differences (Hedge's g) of accuracies and signal detection estimates between sensory visual cortex TMS and control conditions. The width parameter of each Cauchy prior was calculated to correspond to a 90% cumulative probability of values in the distribution laying within the expected effect size. By considering the overall effect size (*g* = .58), the effect size for early TMS (up to 200 ms; *g* = .80), and the effect size for late TMS (after 200 ms; *g* = .50) from previous meta-analytic work (Phylactou et al., 2021), the width parameter of the Cauchy distribution was calculated to correspond to 0.092 for the 0 ms condition, to 0.13 for the 200 ms condition, and to 0.08 for the 1000 ms condition, respectively.

Experiment 2. In Experiment 2, the independent variables will be the stimulation site (ipsilateral, contralateral) and the TMS condition (real, sham). As in Experiment 1, the dependent variable will be the estimated detection sensitivity as measured with *d'*. Thus, for Experiment 2 we

will perform four paired t-tests; one t-test between ipsilateral *d'* versus contralateral *d'* for each of

the two TMS timing conditions (200 ms, 1000 ms) only for the real TMS condition, and one paired t-

test between real TMS *d'* versus sham TMS *d'* for each of the TMS timing conditions (200 ms, 1000

ms) across hemispheres. The stimulation site (ipsilateral vs. contralateral) t-test will be performed to

replicate the results of Experiment 1 regarding the involvement of the sensory visual cortex during

early (200 ms condition paired t-test) and late (1000 ms condition paired t-test) VSTM maintenance,

by testing if the difference between ipsilateral *d'* and contralateral *d'* equals to 0 (null hypothesis) or

not (alternative hypothesis). The real TMS *d'* versus sham TMS *d'* comparison will test the effects of

stimulation across hemispheres to provide evidence for the involvement of the sensory visual cortex

during early (200 ms condition paired t-test) and late (1000 ms condition paired t-test) VSTM

maintenance, by testing if the difference between real TMS *d'* and sham TMS *d'* equals to 0 (null

hypothesis) or not (alternative hypothesis). Further, it will indicate whether the analyses between

the stimulation site (ipsilateral vs. contralateral) were insufficient to detect a TMS effect (e.g., if

evidence is found in favor of the null hypotheses for ipsilateral vs. contralateral tests and evidence

for an alternative hypothesis is found in the real TMS vs. sham TMS tests), or if the sensory visual

cortex is not involved during early and/or late VSTM maintenance (evidence in favor of the null

hypotheses in both ipsilateral vs. contralateral and real vs. sham TMS tests).

The priors which will be used for the paired t-tests are described as a Cauchy distribution

centered around 0 with a width set to 0.13 for the 200 ms condition and 0.08 for the 1000 ms

condition, as estimated by the results of recent meta-analytic evidence (Phylactou et al., 2021),

which reported a standardised effect size for early TMS (up to 200 ms; *g* = .99) and for late TMS

(after 200 ms; *g* = .65).

Data filtering. Participants with an overall accuracy close to chance levels (< 60% accuracy)

in Experiments 1 and 2 will be excluded from analyses and replaced. The data of such participants

will not be used during Bayesian sample updating nor for our main analyses. Additionally, we will

exclude and replace participants in the case of technical or other difficulties, if data loss is greater

than 20% of the total experimental trials. Further, the slowest and fastest responses will be removed

from the analyses. To do so, we will filter each participant's responses and exclude any data that

concern response times which are further than 3 standard deviations away from each participant's

mean reaction time. Assuming that the reaction times of each participant are normally distributed,

we expect less than 0.5% of the data of each participant to be excluded from the main analyses.

Data and code availability

The authors are committed to sharing all data, code and materials used in this study upon

Stage 2 acceptance.

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Author contributions

PP and NK contributed equally to the conceptualization of the study. The final experimental design was completed with the support of AS. Equal contributions are expected for the experimental paradigm programming, data collection, and data analysis. PP prepared the original draft while NK and AS reviewed and edited the manuscript. NK acquired funding for the project.

Competing interests

The authors declare no competing interests.

Tables and Figures

Table 1: Design Table				
Question	**Hypothesis**	**Sampling plan**	**Analysis Plan**	**Interpretation given to different outcomes**
Experiment 1				
Is sensory visual cortex necessary during the perceptual processing of information in visual short-term memory?	H1: Given the established role of the sensory visual cortex during visual perception, we hypothesize that evidence for a difference between the ipsilateral and contralateral conditions will be present when sensory visual cortex TMS is induced at 0 ms (i.e., during memory sample presentation).	Sample updating with a stopping rule set at $BF_{10} > 6$ or $< 1/6$ for all three paired t-tests. Healthy individuals with normal or corrected to normal color vision. To ensure counterbalancing a minimum of 20 participants will be recruited. Due to time and resource constraints a maximum of 40	Paired t-test between the ipsilateral and contralateral 0 ms condition on *d'* using a Cauchy prior centered around zero and width $r = .092$ ($B_{C(0,.092)}$).	The 0 ms condition works as an outcome neutral test or positive control. Evidence in support of the alternative hypothesis (i.e. TMS during the presentation of the memory sample affects VSTM performance) will indicate that our methods are reliable to detect a sensory visual cortex TMS effect between ipsilateral and contralateral stimulation. In such case, the sample mean distribution will indicate whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Given the well-established role of the sensory visual cortex in perception, evidence in support of the null hypothesis (i.e. VSTM performance not affected by sensory visual cortex stimulation during presentation of the memory sample) will indicate that the methods implemented might be insufficient to detect a TMS effect (e.g., possibly due to TMS affecting both hemispheres and/or due to feedforward mechanisms of the sensory visual cortex), which will be further explored with the addition of the sham TMS condition in Experiment 2.

Is sensory visual cortex necessary during the early maintenance of information in visual short-term memory?	H2: We hypothesise that evidence for a difference between the ipsilateral and contralateral conditions will be present when sensory visual cortex TMS is induced at 200 ms.	participants will be recruited.	Paired t-test between the ipsilateral and contralateral 200 ms condition on *d'*, $B_{C(0,.13)}$ prior.	The 200 ms TMS condition will provide evidence in support for or against the involvement of the sensory visual cortex during early information maintenance in VSTM. If evidence for the alternative hypothesis is found, the sample mean distribution will indicate whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate either that the sensory visual cortex is not involved in early VSTM maintenance or that ipsilateral versus contralateral comparisons are insufficient to detect a sensory visual cortex TMS effect. If evidence for a null hypothesis is found between the ipsilateral and contralateral condition but evidence for the alternative is found in H5 (see also *Interpretation given to different* outcomes for Experiment 2), it indicates that TMS effects are undetectable between the ipsilateral and contralateral conditions with our methods (e.g., due to TMS spreading to both hemispheres and/or due to feedforward mechanisms). If evidence in favor of the null hypotheses is found for both H2 and H5, this will indicate that sensory visual cortex is not involved in early VSTM maintenance.
Is the sensory visual cortex necessary during the late maintenance of information in visual short-term memory?	H3: We hypothesise that evidence for a difference between the ipsilateral and contralateral conditions will be present when sensory visual cortex TMS is induced at 1000 ms.		Paired t-test between the ipsilateral and contralateral 1000 ms condition on *d'*, $B_{C(0,.08)}$ prior.	The 1000 ms TMS condition will provide evidence in support for or against the involvement of the sensory visual cortex during late information maintenance in VSTM. If evidence for the alternative hypothesis is found, the sample mean distribution will indicate whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate either that the sensory visual cortex is not involved in late VSTM maintenance or that our methods of ipsilateral versus contralateral comparisons are insufficient to detect a sensory visual cortex TMS effect. If evidence for a null hypothesis is found between the ipsilateral and contralateral condition but evidence for the alternative is

				found in H7 (see also *Interpretation given to different outcomes for Experiment 2*), it indicates that TMS effects are undetectable between the ipsilateral and contralateral conditions with our methods. If evidence in favor of the null hypotheses is found for both H3 and H7, it indicates that sensory visual cortex is not involved in late VSTM maintenance.
Experiment 2				
Is the sensory visual cortex necessary during the early maintenance of information in visual short-term memory?	H4: We aim to replicate the effects of Exeriment 1 (H2) for the difference between the ipsilateral and contralateral conditions when sensory visual cortex TMS is induced at 200 ms.	Sample updating with a stopping rule set at $BF_{10} > 6$ or $< 1/6$ for all four paired t-tests. Healthy individuals with normal or corrected to normal color vision. To ensure counterbalancing a minimum of 20 participants will be recruited. Due to time and resource constraints a maximum of 40 participants will be recruited.	Paired t-test between the ipsilateral and contralateral 200 ms condition on d', $B_{C(0,.13)}$ prior.	Evidence for the alternative hypothesis indicates an involvement of the sensory visual cortex in early VSTM maintenance, with the sample mean distribution indicating whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate either that the sensory visual cortex is not involved in early VSTM maintenance or that our methods of ipsilateral versus contralateral comparisons are insufficient to detect a sensory visual cortex TMS effect. However, if evidence for a null hypothesis is found between the ipsilateral and contralateral condition but evidence for the alternative is found in H5, then evidence in favor of the null hypothesis indicates that TMS effects are undetectable between the ipsilateral and contralateral conditions. If evidence in favor of the null hypotheses is found for H2, H4 and H5, it indicates that sensory visual cortex is not involved in early VSTM maintenance.
	H5: We hypothesise that evidence for a difference between the real and sham TMS conditions will be present when sensory visual cortex TMS is induced at 200 ms.		Paired t-test between the real and sham 200 ms TMS condition on d' across hemispheres, $B_{C(0,.13)}$ prior.	Evidence for the alternative hypothesis indicates an involvement of the sensory visual cortex in early VSTM maintenance. If evidence is found between real and sham sensory visual cortex TMS across hemispheres, but no evidence is found between the ipsilateral and contralateral conditions (H2, H4), then hemisphere comparisons alone were insufficient to detect the TMS effect.

				The sample mean distribution indicating whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate that the sensory visual cortex is not involved in early VSTM maintenance.
Is the sensory visual cortex necessary during the late maintenance of information in visual short-term memory?	H6: We aim to replicate the effects of Exeriment 1 for the difference between the ipsilateral and contralateral conditions when sensory visual cortex TMS is induced at 1000 ms.		Paired t-test between the ipsilateral and contralateral 1000 ms condition on d', $B_{C(0,.08)}$ prior.	Evidence for the alternative hypothesis will indicate an involvement of the sensory visual cortex in late VSTM maintenance, with the sample mean distribution indicating whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate either that the sensory visual cortex is not involved in late VSTM maintenance or that our methods of ipsilateral versus contralateral comparisons are insufficient to detect a sensory visual cortex TMS effect. If evidence for a null hypothesis is found between the ipsilateral and contralateral condition but evidence for the alternative is found in H7, then evidence in favor of the null hypothesis indicates that TMS effects are undetectable between the ipsilateral and contralateral conditions with our methods. If evidence in favor of the null hypotheses is found for H3, H6 and H7, it will indicate that the sensory visual cortex is not involved in early VSTM maintenance.
	H7: We hypothesise that evidence for a difference between the real and sham TMS conditions will be present when sensory visual cortex TMS is induced at 1000 ms.		Paired t-test between the real and sham 1000 ms condition on d' across hemispheres, $B_{C(0,.08)}$ prior.	Evidence for the alternative hypothesis will indicate an involvement of the sensory visual cortex in late VSTM maintenance. If evidence is found between real and sham TMS across hemispheres, but no evidence is found between the ipsilateral and contralateral conditions (H3, H6), it will indicate that hemisphere comparisons alone were insufficient to detect the TMS effect.

				The sample mean distribution indicating whether the effects of TMS are inhibitory (sample mean < 0) or facilitatory (sample mean > 0). Evidence for the null hypothesis will indicate that the sensory visual cortex is not involved in late VSTM maintenance.

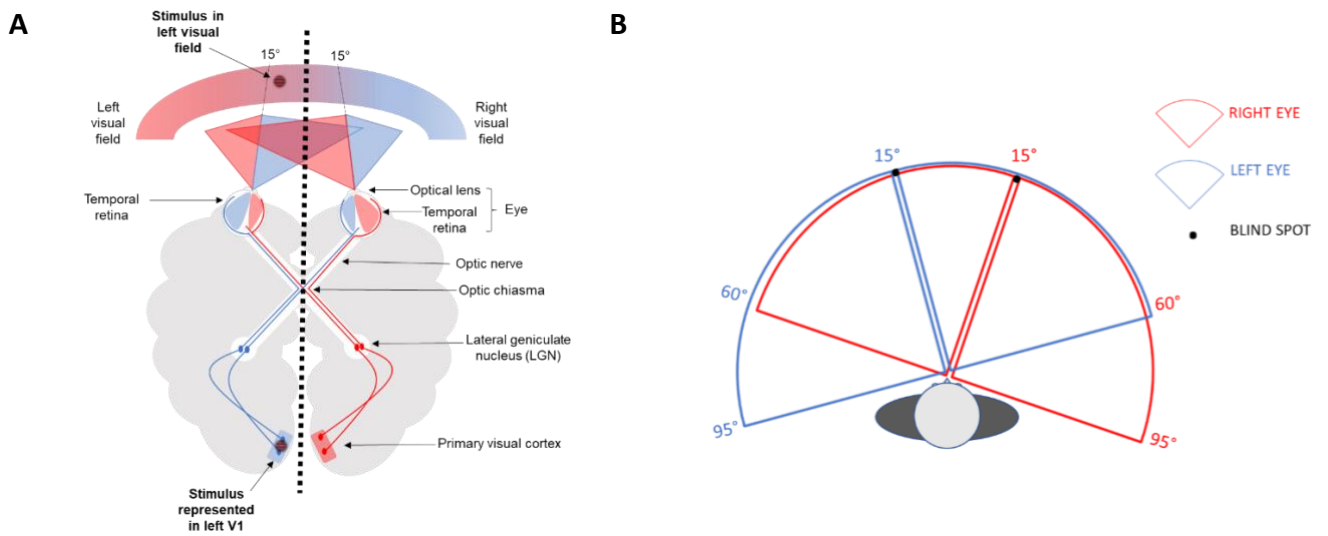**Figure 1:** Stimuli and experimental procedure

Fig.1 (A) In dichoptic presentation (represented by black vertical dotted line), a stimulus presented on the left visual field cannot be perceived by the right eye and it is therefore represented only in the ipsilateral V1 (i.e., left V1 in this example). (B) Visual field angle of the left and right eye. Stimuli presented within 15° of visual angle off of fixation are perceived by both eyes.
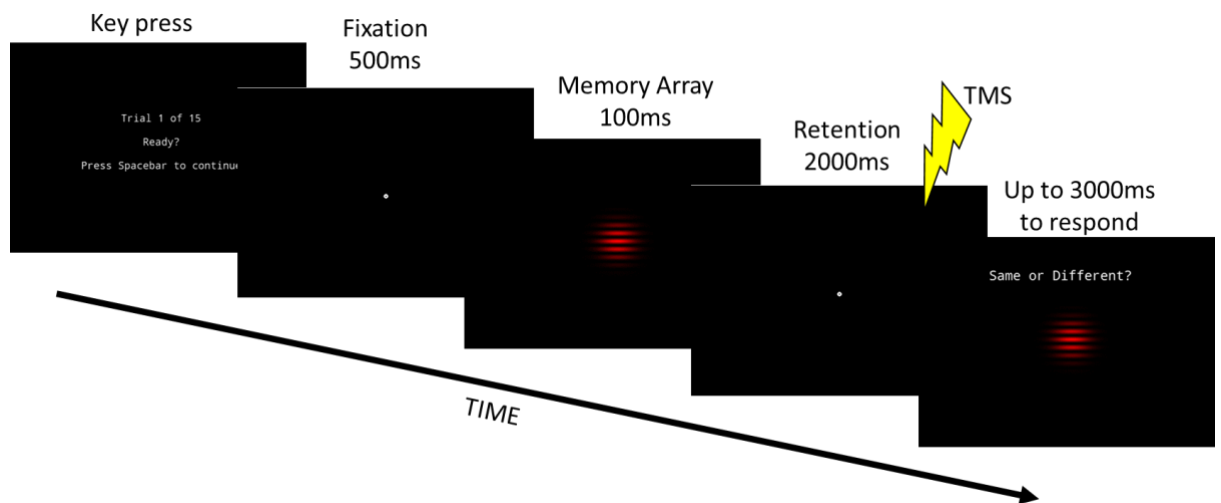
Figure 2: Stimuli and experimental procedure

Fig.2 An example of the delayed change-detection task used in Experiments 1 and 2. The trial begins with a screen indicating the trial number, requesting a keypress to proceed. This is followed by a 500 ms fixation dot. Next, the memory array, consisting of either a red or blue Gabor patch, is shown for 100 ms and participants are asked to memorise its orientation. From the memory array onset, a 2000 ms retention period is presented. During the retention phase, double-pulse TMS is induced at either the left or right sensory visual cortex. In Experiment 1, stimulation is induced at 0 ms, 200 ms, or 1000 ms after the memory array onset. In Experiment 2, either real or sham stimulation is induced at 200 or 1000 ms after the memory array onset. Following the retention period, a probe stimulus is presented at the centre of the screen for up to 3000 ms (or until a respose is given), where participants have to respond whether it matches the remembered stimulus or not.